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The impacts of historical barriers on floristic patterns of plant groups with different dispersal abilities in the Ryukyu Archipelago, Japan

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1 **THE IMPACTS OF HISTORICAL BARRIERS ON FLORISTIC PATTERNS OF**

2 **PLANT GROUPS WITH DIFFERENT DISPERSAL ABILITIES IN THE RYUKYU**

3 **ARCHIPELAGO, JAPAN**

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17 *ABSTRACT.* - The effects of historical barriers in biogeographical patterns are expected to

18 persist differently depending on dispersal abilities of organisms. We tested two hypotheses that

19 plant groups with different dispersal abilities display different floristic patterns, and that

20 historical barriers can explain floristic differentiation patterns in plants with low dispersal

21 ability but not in plants with higher dispersal ability, in the seed plant flora of the Ryukyu

22 Archipelago. This area is biogeographically interesting because several similar floristic

23 differentiation patterns have been proposed, all of which are primarily explained by two

24 historical barriers, the Tokara Tectonic Strait (Tokara Gap) and the Kerama Gap, which arose

25 during the formation of the islands. We calculated floristic dissimilarity distance among 26

1   islands based on data sets for three dispersal-ability classes. Clustering analyses based on the

2   floristic dissimilarity distance generated similar floristic patterns regardless of dispersal-ability

3   class. We propose that because the landscape resistance is so strong that migration of plants is

4   severely restricted regardless of their dispersal abilities, the similar floristic differentiation

5   patterns are generated. Multivariate regression analyses using Mantel's randomization test

6   indicated that floristic differentiations among islands were explained by the both effects of the

7   historical barriers and geographic distance in all dispersal-ability classes. Significance of the

8   historical barriers is not determined by the plant dispersal abilities but presumably by the spatial

9   distribution of the islands, stochastic dispersals, and time since the formation of the barriers.

10

11   ***KEY WORDS.*** - Dispersal ability, floristic pattern, historical barrier, landscape resistance,

12   similarity distance.

13

14

15   **INTRODUCTION**

16

17   The interactions between historical and current processes that shape biogeographic patterns are

18   a key component of biogeographical studies (e.g., Candolle, 1820; Good, 1974; Brown &

19   Gibson, 1983; Cox & Moore, 1993; Crisci et al., 2003). In historical biogeography,

20   biogeographic patterns are explained based on past processes that have persisted over very long

21   periods of time, such as geological barriers formed by tectonic movements over millions of

22   years (Crisci et al., 2003). However, current processes such as ongoing dispersals can affect or

23   obscure evidence of historical patterns with migration across historical barriers (Wolf et al.,

24   2001; Giller et al., 2004). Therefore, historical barriers and current dispersals compete in

25   shaping biogeographic patterns; however, their relative importance is expected to vary

1   depending on abiotic and biotic factors such as the spatial configuration of habitats and the

2   dispersal ability of organisms. Increased knowledge of the shifting relative importance in

3   relation to these factors would enhance our understanding of processes that structure

4   biogeographic patterns. The Ryukyu Archipelago is a suitable study area for such studies.

5

6   The Ryukyu Archipelago is an assemblage of continental islands located between Kyushu

7   Island of Japan and Taiwan (Fig. 1). This area is biogeographically interesting because several

8   similar floristic differentiation patterns have been proposed, all of which are primarily

9   explained by two historical barriers, the Tokara Tectonic Strait (Tokara Gap) and the Kerama

10   Gap, which arose during the formation of the islands (Hara, 1959; Good, 1974; Maekawa,

11   1974; Shimabuku, 1984; Takhtajan, 1986; Kitamura et al., 1994). However, it is expected that

12   plant groups whose seeds/fruits exhibit differing dispersal abilities display different floristic

13   patterns because the effects of the historical barriers are dependent on dispersal ability. That is,

14   a lower dispersal ability results in a greater amount of time that the historical effects are able to

15   persist, whereas a higher dispersal ability results in fewer historical effects (Nekola & White,

16   1999). Therefore, it is thought that historical barriers can explain floristic differentiation

17   patterns in plants with low dispersal ability, but not in plants with higher dispersal ability. In the

18   latter case, it is expected that without an effective barrier to dispersal, the floristic

19   differentiation would be correlated to the geographic distance between the islands, and that the

20   floristic pattern is explained by this spatial effect.

21

22   To test this hypothesis, we compiled the distribution records of seed plants and grouped them

23   into three dispersal-ability classes for each island of the Ryukyu Archipelago to examine the

24   floristic patterns for each dispersal-ability class. We then used a multivariate approach to

25   examine how the significance of the effects of the two historical barriers and the geographic

1   distance differ with various dispersal-ability classes.

2

3

MATERIAL AND METHODS

5

Study area

7

8   The Ryukyu Archipelago is thought to have undergone extensive changes in land configuration

9   during the Cenozoic, and there was more than one period of landbridge connection between the

10   islands and surrounding landmasses (Kyushu to the north, and southeastern China via Taiwan to

11   the south). This enhanced the range expansion of various lineages of terrestrial organisms in

12   this region (Hatusima, 1975; Ota, 1998; Chiang & Schaal, 2006). It is proposed that by the

13   Pliocene or early Pleistocene, the landbridge was segmented at two areas called the Tokara Gap

14   and the Kerama Gap, where the sea is currently more than 1000 m deep (Kawana, 2002), as a

15   result of tectonic movements and eustatic sea-level rise. It is thought that the islands have not

16   since been connected across the gaps, even during the Quaternary glacial sea-level minima (Ota,

17   1998). Given this geohistory, many reports have demarcated the flora at one or both of the gaps

18   (e.g., Hara, 1959; Good, 1974; Maekawa, 1974; Shimabuku, 1984; Takhtajan, 1986; Kitamura

19   et al., 1994). For example, Takhtajan (1986) placed the demarcation line of the

20   Japanese–Korean and Ryukyu provinces and that of the Ryukyu and Taiwanian provinces at the

21   Tokara and Kerama Gaps, respectively. In addition, Good (1974) and Kitamura et al. (1994)

22   regarded the Tokara Gap as the demarcation between the Sino–Japanese Region of the Boreal

23   Kingdom and the Continental Southeast Asiatic Region of the Paleotropical Kingdom.

24

25   The spatial arrangement of the 26 islands examined in this study is shown in Fig. 1. These

4

1   islands were selected because of the availability of reliable lists of seed plant flora. Based on the

2   two gaps, the islands of the Ryukyu Archipelago are divided into three groups: the islands 1 to

3   12, 13 to 22, and 23 to 26 belong to the northern, central, and southern Ryukyus, respectively.

4   The Ryukyu Archipelago is in the subtropics, or the transition from tropical to warm temperate

5   zones (Good, 1974). The climate is moderate throughout the year with a mean temperature of

6   approximately 15°C during the winter and 28°C in summer, and annual precipitation exceeds

7   2000 mm with no dry season. Therefore, the islands are covered in well-developed

8   broad-leaved evergreen forests (Maekawa, 1974).

9

10   **Floristic data editing**

11

12   The vascular plant flora of the Ryukyu Archipelago comprises approximately 1800 species

13   (Hatusima & Nackejima, 1979); however, detailed records of each species for each island have

14   not been compiled in one source. We referred to six literature sources for distribution records of

15   native plants on the 26 islands (Hatusima & Amano, 1974, 1994; Hatusima et al., 1975; Niiro &

16   Shinjo, 1989; Hatusima, 1991; Kawakubo & Tagawa, 1991). We compiled data sets for three

17   dispersal-ability classes: high (269 wind-dispersed species with dust seeds and fruits having

18   hairy pappi), low (200 gravity-dispersed species mostly with acorns and dehiscent fruits), and

19   intermediate (224 bird-dispersed species mostly with sap-fruits). Each of the three classes

20   included a similar number of species. Estimation of dispersal abilities was based on dispersal

21   vectors estimated on the basis of seed/fruit morphology (e.g., Brown & Gibson, 1983).

22   Infraspecific taxa were not separated to avoid taxonomic incongruence among the literature

23   sources and to avoid giving intra- and inter-specific differences equal weighting.

24

25   For each dispersal-ability class, the pairwise floristic similarity between islands was calculated

1   using Simpson's similarity index (SI); SI = $\gamma \beta^{-1}$, $(\alpha > \beta)$, where γ is the number of species

2   shared between two islands, and α and β are the numbers of species on each of the two islands

3   (Simpson, 1943). SI is one of the most frequently used similarity indices in biogeographic

4   analyses (Brown & Gibson, 1983), and we selected this index because it does not give an

5   improperly low similarity value when the areas (and hence the numbers of species) being

6   compared differ greatly (Balgooy, 1971). Floristic dissimilarity distance was calculated by

7   subtracting the value of SI from 1.

8

9   **Historical and spatial variables**

10

11 The historical effect of the Tokara Gap was expressed as a categorical matrix using dummy

12 variables; a value of 1 was given to matrix elements comparing two islands crossing over the

13 Tokara Gap, and a value of 0 was given to matrix elements comparing two islands on either side

14 of the Tokara Gap. The matrix of the Kerama Gap was constructed in the same manner. This is

15 because the proposed dates of the formation of the gaps are very approximate (Ota, 1998),

16 meaning that we cannot use these dates as accurate and reliable variables. Pairwise geographic

17 distance (km) among the islands was calculated based on the geological coordinates at the

18 highest points of each island (range = 11.3–1042.0 km; average distance = 353.2 km; SD =

19 284.0 km).

20

21   **Data analyses**

22

23 To illustrate the floristic biogeographic pattern in each dispersal-ability class, clustering

24 analyses of the islands were conducted based on floristic dissimilarity distances using the

25 unweighted pair group method with arithmetic mean (UPGMA; Sneath & Sokal, 1973) with

6

1   PAUP* 4.0b10 (Swofford, 2002).

2

3   To examine the significance of the effects of the Tokara and Kerama Gaps and the inter-island

4   geographic distance on the variation in the floristic dissimilarity distance, we conducted partial

5   Mantel tests. A Mantel test is used to test the statistical significance of correlations of distance

6   matrices, where matrix elements are not independent, by randomization (Mantel, 1967; Smouse

7   et al., 1986; Legendre et al., 1994). Partial Mantel tests are used to conduct partial linear

8   regression analyses using a response matrix and two explanatory matrices to test the correlation

9   between the response variable and one of the explanatory variables while controlling for the

10   effect of the other explanatory variable to remove spurious correlation (Legendre, 2000; Bonnet

11   & Peer, 2002; Tuomisto et al., 2003; Legendre et al., 2005; Lichstein, 2007). We conducted

12   partial Mantel tests of the floristic dissimilarity distance with two pairs of explanatory variables,

13   Tokara Gap and geographic distance, and Kerama Gap and geographic distance, using the

14   software program 'zt' with 10000 randomizations (Bonnet & Peer, 2002).

15

16   To estimate the geographic extent of the significant correlation between the floristic

17   dissimilarity distance and the geographic distance, we calculated a correlation coefficient r for

18   given distance classes using GeneAlEx 6 software (Peakall & Smouse, 2006). Distance class

19   sizes were determined to include a similar number of pairwise comparisons (32 or 33 island

20   pairs) within each distance class. The calculated correlation coefficients were plotted as a

21   function of geographic distance. Statistical significance of r was tested by 1000 randomizations

22   for the null hypothesis of no correlation.

23

24

25   **RESULTS**

7

1

2 **Floristic distance and clustering of islands**

3

4 Mean values of the pairwise floristic dissimilarity distances were 0.240 (range = 0–0.576) in

5 high, 0.187 (0–0.485) in intermediate, and 0.260 (0–0.641) in low dispersal-ability classes.

6 UPGMA clusterings in three dispersal-ability classes are shown in Fig. 2. Seen in a broad

7 perspective, the clustering patterns were similar and approximately congruent with the

8 geographic arrangement of the islands in the archipelago. In all three classes, the islands of each

9 of the northern, central, and southern Ryukyus were separated, with some exceptional small

10 islands (islands 13–15, 26). Among the three regions, the islands of the central and southern

11 Ryukyus were more closely connected to each other than to the islands of the northern Ryukyus.

12

13 **Regression analyses**

14

15 The results of the partial Mantel tests are shown in Table 1. In the high-dispersal ability class,

16 the partial regression of the floristic distance matrix on the matrix of the Tokara Gap,

17 controlling the effect of the geographic distance, was positive and significant ($r = 0.31$, p =

18 0.0001; in partial Mantel tests of this study, significance level 5% with Bonferroni adjustment

19 was $p = 0.05/12 = 0.0042$), and so was the partial regression of the floristic distance matrix on

20 the geographic distance, controlling the effect of the Tokara Gap ($r = 0.31$, $p = 0.0002$). The

21 partial regression of the floristic distance matrix on the matrix of the Kerama Gap, controlling

22 the effect of the geographic distance, was negative but not significant ($r = - 0.07$, $p = 0.1876$),

23 whereas the effect of the geographic distance, controlling the effect of the Kerama Gap, was

24 significantly positive ($r = 0.29$, $p = 0.0002$). The results for the intermediate and low

25 dispersal-ability classes were generally in accordance with one another. Specifically, the partial

8

1   regression of the floristic distance matrix on the matrix of the Tokara Gap, controlling the effect

2   of the geographic distance, was significantly positive (intermediate: $r = 0.44$, $p = 0.0002$; low: r

3    $= 0.18$, $p = 0.0037$) and vice versa (intermediate: $r = 0.38$, $p = 0.0001$; low: $r = 0.49$, $p = 0.0001$).

4   The partial regression of the floristic distance matrix on the matrix of the Kerama Gap,

5   controlling the effect of the geographic distance, was significantly negative (intermediate: $r = $ -

6   0.28, $p = 0.0003$; low: $r = - 0.31$, $p = 0.0006$) but the effect of the geographic distance,

7   controlling the effect of the Kerama Gap, was significantly positive (intermediate: $r = 0.49$, $p = $

8   0.0001; low: $r = 0.55$, $p = 0.0001$).

9

10   **Geographic extent of spatial correlation**

11

12   As shown in Figure 3, the analyses examining the geographic extent of the significant

13   correlation between the floristic dissimilarity distance and the geographic distance generated

14   very similar patterns in the three dispersal-ability classes. Specifically, the correlation

15   coefficients were positive and significant in the first four distance classes (56, 104, 139, 186

16   km), with an x-intercept of approximately 250 km. The geographic extent of positive

17   correlation can be influenced by the chosen distance class size (Double et al., 2005); however

18   changing distance class sizes generated similar patterns (data not shown).

19

20

21   **DISCUSSION**

22

23   **Dispersal ability and floristic patterns**

24

25   The UPGMA analyses generated similar clustering patterns regardless of dispersal-ability class.

1   This result rejects the hypothesis that plant groups with different dispersal abilities exhibit

2   different floristic patterns. Biogeographic patterning results from each organism's migration,

3   which is a function of its dispersal ability and landscape resistance to the movement of the

4   organism (Nekola & White, 1999). Therefore, the similar floristic patterns observed here are

5   likely explained from these two viewpoints.

6

7   One explanation for our results is that the classification of dispersal ability was not adequate

8   and there was no significant difference in the potential dispersal distances among the three

9   classes. It is difficult to accurately estimate the dispersal ability of plants because evidence of

10 dispersal, especially such a long-distance dispersal as to cross over sea, is not available for most

11 plant species (Cain, 1974). Also, with respect to long distance dispersal, estimating dispersal

12 abilities based on seed/fruit morphology might be misleading because the morphological

13 adaptations of seeds/fruits that are typically used to identify the standard dispersal vector tend

14 to govern short-distance dispersal but do not necessarily constitute the main mechanism

15 responsible for long-distance dispersal (Nathan, 2006). Long-distance dispersal can occur by

16 means of multiple stochastic dispersal vectors, even in the absence of specific adaptations for

17 each vector (Bullock & Clarke, 2000; Myers et al., 2004). Conversely, some analyses

18 examining the relationships between plant dispersal abilities and decrease-rate of floristic

19 similarity with geographic distance have indirectly illustrated that plants with seeds/fruits

20 adapted to bird-dispersal are more dispersal-limited than plants adapted to wind-dispersal

21 (Nekola & White, 1999; Tuomisto et al., 2003). Therefore, classification of the plant dispersal

22 abilities based on the seed/fruit morphology is not necessarily unreasonable. Assuming that our

23 dispersal-ability classification was accurate, a second explanation for our results must consider

24 the effect of landscape resistance.

25

1 Given that the landscape resistance is common to the analyses of the three dispersal-ability

2 classes, it is likely responsible for the similar results in our analyses. Landscape resistance is

3 caused by spatial configuration, particularly size and isolation of habitats. The more isolated

4 and/or the smaller the habitat, the less effective dispersal will be (Nekola & White, 1999;

5 Sklenář & Jørgensen, 1999). For example, in North American spruce-fir forests, isolated

6 habitats restricted to the highest peaks, which are analogous to the habitats of islands, exhibit

7 much stronger landscape resistance than more contiguous habitats (Nekola & White, 1999). In

8 the Ryukyu Archipelago, it is very plausible that the isolated distribution of relatively small

9 islands is causing strong landscape resistance. As shown in Fig. 3, the distance at which the

10 correlation between floristic dissimilarity distance and geographic distance becomes effectively

11 zero was approximately 200 km, regardless of the dispersal-ability class. This means that the

12 geographic extent of the correlation is confined to a comparatively small area while the

13 archipelago extends for more than 1300 km. We propose that because the landscape resistance

14 is so strong that migration of plants is severely restricted regardless of their dispersal abilities,

15 the plant groups whose potential dispersal distances in a contiguous landscape are different

16 generate similar differentiation patterns.

17

18   **Significance/insignificance of historical effects**

19

20 The partial Mantel tests indicated that the floristic differentiations among islands were

21 explained by both historical effect and geographic distance in all three dispersal-ability classes.

22 This result rejects the hypothesis that historical barriers can not explain floristic differentiation

23 patterns in plants with higher dispersal ability. The UPGMA analyses indicated that the

24 northern, central, and southern Ryukyus were essentially separated. This separation pattern

25 seems to be consistent with the hypotheses of the preceding studies, which explain the floristic

11

1   differentiation pattern primarily by the historical gaps (Hara, 1959; Good, 1974; Maekawa,

2   1974; Shimabuku, 1984; Takhtajan, 1986; Kitamura et al., 1994). However, our partial Mantel

3   tests indicated that geographic distance and the Tokara Gap have exhibited significantly

4   positive effects but that the effects of the Kerama Gap were insignificant or significantly

5   negative. The significantly positive effect of the Kerama Gap was spurious. Note that the

6   geographic distances between islands across the Kerama Gap are much larger than those of the

7   Tokara Gap (the shortest distances across each gap are 227.6 km between islands 22 and 23 and

8   36.6 km between islands 12 and 13; Fig. 1). However, the UPGMA analyses indicated that the

9   islands of the central and southern Ryukyus were more closely connected to each other than to

10   the islands of the northern Ryukyus. Therefore, the explanation for the insiginificant effect of

11   the Kerama Gap in high dispersal-ability class is that the floristic dissimilarity distance across

12   the Kerama Gap was no more that what was explained by the effect of the accompanying large

13   geographic distance. Similarly, the explanation for the negative effects in the intermediate and

14   low dispersal-ability classes is that the floristic dissimilarity distance across the gap was less

15   than what was expected from the large geographic distance, for which the effect of the Kerama

16   Gap was adjusted to be negative. This is because that although the significantly positive effect

17   of the Kerama Gap was spurious, the negative effects in intermediate and low dispersal-ability

18   classes could also be spurious because it is unlikely that the formation of the Kerama Gap

19   increased the floristic similarity among the islands across the gap, considering that the

20   landbridge had played a significant role in the migration of the plants (Hatusima, 1975; Chiang

21   & Schaal, 2006). Thus, the effect of the Kerama Gap would actually be positive but

22   indistinguishable compared to the effect of the large geographic distance.

23

24   When we consider that the Tokara Gap is a very narrow strait (the two closest islands across the

25   gap are only 36.6 km apart today), the significant effect of the Tokara Gap requires an

1   explanation as to why ongoing inter-island dispersal has not completely obscured the effect of

2   the past formation of the gap. The duration of the effects of a historical barrier is determined by

3   the amount of time required for organisms to cross it (Nekola & White, 1999). The Tokara Gap

4   is thought to have formed during the Miocene or at the latest in the early Pleistocene, roughly

5   more than two million years ago (Ota, 1998). A recent quantitatively derived understanding of

6   the long-distance dispersal of plants may help us understand the persistence of the historical

7   effects of the Tokara Gap. The expected time for an effective dispersal, i.e., the successful

8   establishment of one reproductive individual is calculated as the inverse of the product of seed

9   arrival probability and seed-to-adult survival probability (Clark et al., 1999). For example, with

10 a hypothetical source population (10^6 individuals, each with an annual fecundity of 10^4 seeds

11 and with mean dispersal distance of 50 m), the expected time for a single effective dispersal

12 event to occur beyond 150 km is longer than 100 billion years under the mean trend. Conversely,

13 an effective long-distance dispersal event beyond 415 km, expected to occur once in almost

14 10^{13} years under the mean trend, may occur once in 10 years as a result of events that break the

15 rules, such as hurricanes, tornadoes, and tropical cyclones. Similarly, an effective long-distance

16 dispersal event beyond 34 km may occur once in almost 10^8 years under the mean trend but

17 once a year under exceptional conditions (Clark et al., 1999). Long-distance dispersal is an

18 extremely rare phenomenon even at the scale of a few tens of km or a few hundred km, although

19 nonstandard mechanisms may help realize it (Nathan, 2006). Although these are rough

20 estimates for certain types of plants, they still serve as useful references. The time required for

21 long-distance dispersal to cross the Tokara Gap under the mean trend would be much longer

22 than the time since the formation of the gap (> 2 million years), although this time would have

23 allowed some species to cross the gap with nonstandard mechanisms such as summer typhoons.

24 Thus, it is likely that the historical effects of the Tokara Gap have been preserved because of the

25 rarity of long-distance dispersal across the gap beyond 36.6 km under the mean trend with the

13

1   time being limited. Therefore, the significance of the historical barriers is not determined by the

2   plant dispersal abilities but presumably by the spatial distribution of the islands, stochastic

3   dispersals, and time since the gap formation.

4

5

6   **ACKNOWLEDGEMENTS**

7

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15

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9

1 **Table 1.** Summary of partial Mantel tests of floristic dissimilarity distance in three

2 dispersal-ability classes. The tests were conducted with two pairs of explanatory variables,

3 Tokara Gap-geographic distance, and Kerama Gap-geographic distance. The significance was

4 tested with 10000 randomizations. Significance level 5% with Bonferroni adjustment for

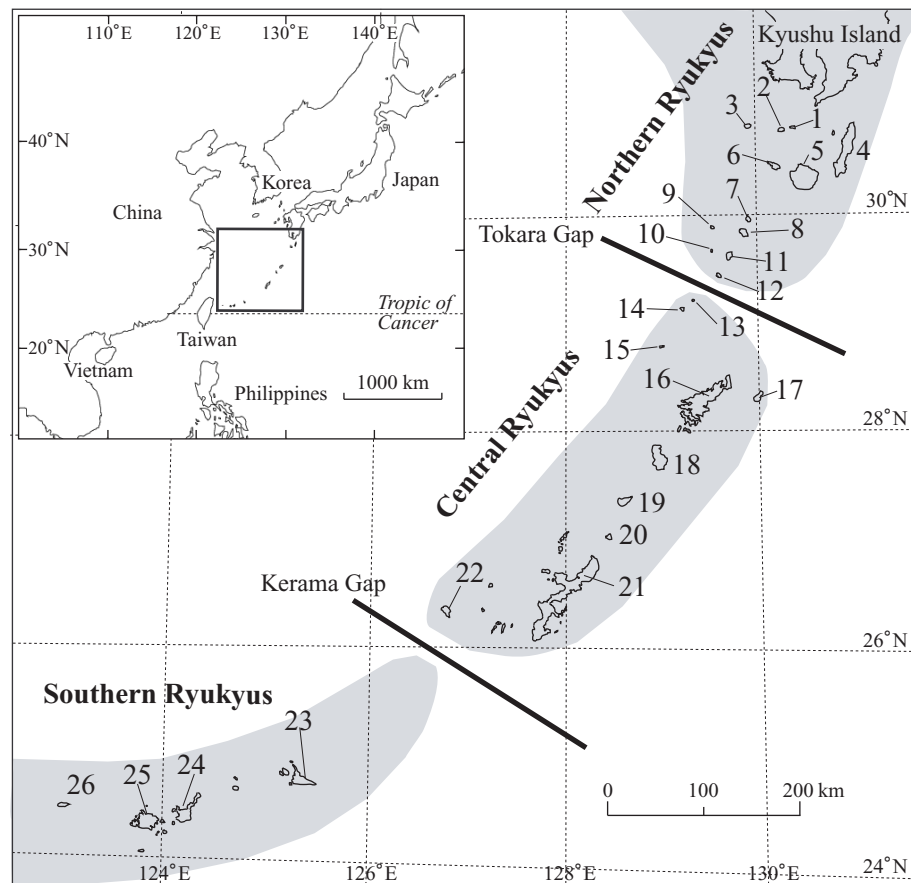5 multiple comparisons was p = 0.05/12 = 0.0042. * = significant, n.s. = not significant

6

7

8

Dispersal ability	Explanatory variable	Controlled variable	r	p
High	Tokara	Distance	0.31	0.0001*
	Distance	Tokara	0.31	0.0002*
	Kerama	Distance	-0.07	0.1876[n.s.]
	Distance	Kerama	0.29	0.0002*
Intermediate	Tokara	Distance	0.44	0.0002*
	Distance	Tokara	0.38	0.0001*
	Kerama	Distance	-0.28	0.0003*
	Distance	Kerama	0.49	0.0001*
Low	Tokara	Distance	0.18	0.0037*
	Distance	Tokara	0.49	0.0001*
	Kerama	Distance	-0.31	0.0006*
	Distance	Kerama	0.55	0.0001*

19

1 **FIGURE LEGENDS**

2

3 Fig. 1. Location of the Ryukyu Archipelago in East Asia and distribution of the 26 islands

4 analyzed in the archipelago. Segregation of the archipelago into the northern, central, and

5 southern Ryukyus by the Tokara and Kerama Gaps is shown. Shaded areas indicate land

6 configuration in the early Pleistocene after segmentation of the landbridge by the formation of

7 the gaps, following Ota (1998). The names and the coordinates at the highest peaks (N, E) of the

8 islands are as follows; 1, Takeshima (30° 48′, 130° 25′); 2, Ioujima (30° 47′, 130° 18′); 3,

9 Kuroshima (30° 49′, 129° 56′); 4, Tanegashima (30° 38′, 130° 58′); 5, Yakushima (30° 20′, 130°

10 30′); 6, Kuchinoerabujima (30° 26′, 130° 13′); 7, Kuchinoshima (29° 58′, 129° 55′); 8,

11 Nakanoshima (29° 51′, 129° 51′); 9, Gajajima (29° 54′, 129° 32′); 10, Tairajima (29° 41′, 129°

12 32′); 11, Suwanosejima (29° 38′, 129° 42′); 12, Akusekijima (29° 27′, 129° 35′); 13,

13 Kodakarajima (29° 13′, 129° 19′); 14, Takarajima (29° 08′, 129° 12′); 15, Yokoatejima (28° 48′,

14 128° 59′); 16, Amamioshima (28° 17′, 129° 19′); 17, Kikaijima (28° 18′, 129° 58′); 18,

15 Tokunoshima (27° 46′, 128° 58′); 19, Okinoerabujima (27° 22′, 128° 34′); 20, Yoronjima (27°

16 02′, 128° 25′); 21, Okinawajima (26° 43′, 128° 13′); 22, Kumejima (26° 22′, 126° 46′); 23,

17 Miyakojima (24° 45′, 125° 22′); 24, Ishigakijima (24° 25′, 124° 11′); 25, Iriomotejima (24° 21′,

18 123° 53′); 26, Yonagunijima (24° 27′, 123° 00′).

19

20 Fig. 2. UPGMA clusterings of the 26 islands based on the floristic dissimilarity distance (1 −

21 Simpson's similarity index) in high, intermediate, and low dispersal-ability classes. Island

22 numbers of the northern, central, and southern Ryukyus are colored blue, red and green,

23 respectively. Island names are given in Fig. 1. The scale bars represent floristic dissimilarity

24 distance of 0.1.

25

1   Fig. 3. Plots of the floristic correlation coefficient (r) as a function of geographic distance in

2   high, intermediate and low dispersal-ability classes. Each distance class includes the similar

3   number of pairwise comparisons (32 or 33 island pairs). Dashed lines show the 95% confidence

4   interval for the null hypothesis of no correlation, based on 1000 randomizations.
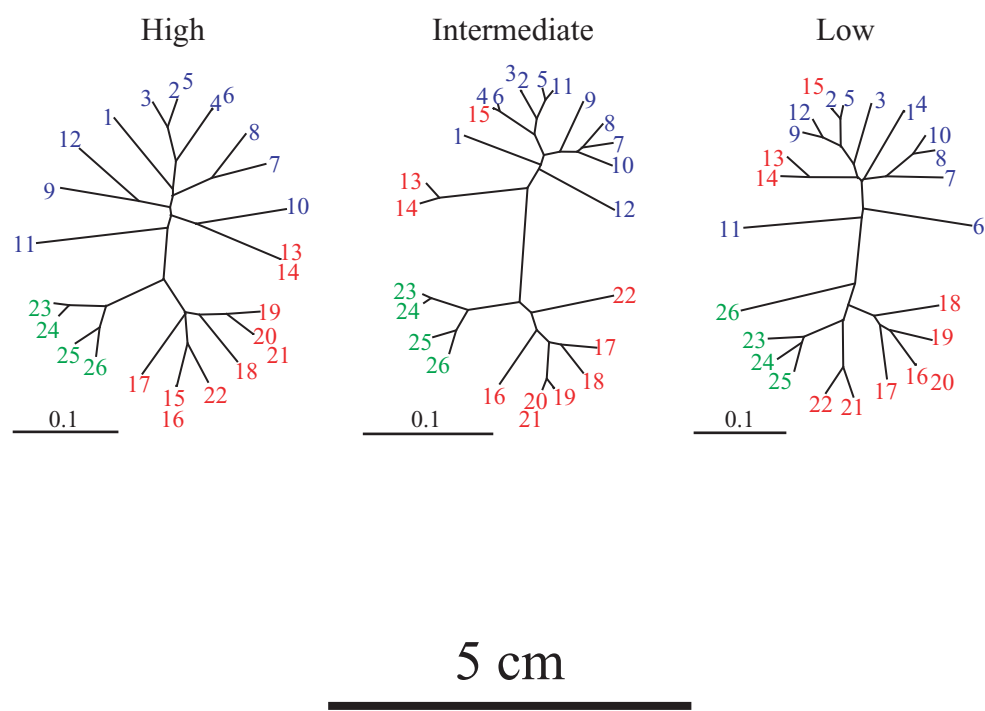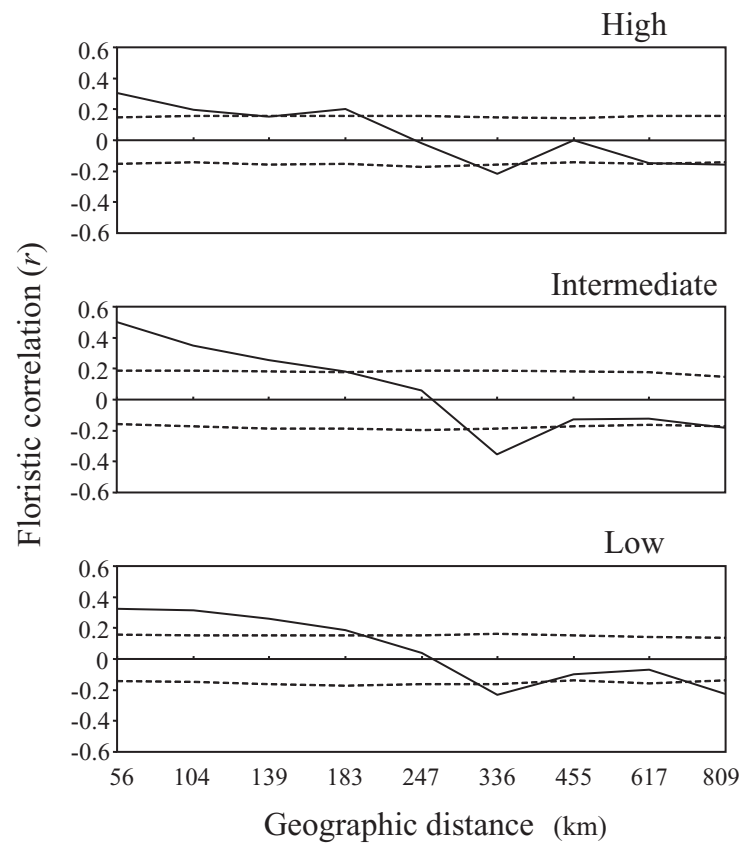
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Fig. 1

Fig. 2

Fig. 3